

ANALYSIS OF TWO PROBLEMATIC NORTH AMERICAN CADDISFLY SPECIES:
OECETIS AVARA (BANKS) AND *OECETIS DISJUNCTA* (BANKS) (TRICHOPTERA:
LEPTOCERIDAE)

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ABSTRACT

Oecetis disjuncta (Banks) has, since 1944, been regarded as possibly conspecific with *Oecetis avara* (Banks). We propose here that these two forms are specifically distinct. Adults, larvae, and pupae of both species are described. In Saskatchewan *O. avara* lives in southern and central regions, while *O. disjuncta* inhabits central and northern regions. Immatures of both species inhabit boreal streams, but those of *O. avara* also inhabit the main branches of the Saskatchewan river system. Because specimens of *O. disjuncta* may, previously, have been misidentified as *O. avara*, some published distribution records for the latter may not be correct. Collection data for specimens examined in this study indicate that both species are widely distributed in North America.

Depuis 1944, on considèrait *Oecetis disjuncta* (Banks) comme un synonyme possible d'*Oecetis avara* (Banks). Nous proposons qu'*O. disjuncta*, bien que morphologiquement similaire à *O. avara*, soit considéré comme une espèce distincte. Nous décrivons les adultes, les larves, et les pupes des deux espèces. En Saskatchewan, *O. avara* occupe les régions du centre et du sud, alors qu'*O. disjuncta* se trouve dans les régions de centre et du nord. Les immatures des deux espèces habitent les affluents secondaires boréaux, mais ceux d'*O. avara* se trouvent aussi dans les branches principales du bassin de la rivière Saskatchewan. Etant donné qu'*O. disjuncta* pourraient avoir été identifiés comme *O. avara*, certaines mentions publiées au sujet de la répartition géographique de cette dernière pourraient être erronées. Les notes de collection des spécimens examinés au cours de cette étude indiquent que les deux espèces sont largement répandues en Amérique du Nord.

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INTRODUCTION

While studying Saskatchewan-collected males of *Oecetis avara* (Banks), we discovered that two distinct color forms are recognizable: one with dark brown body and wings (dark form); and another with yellow body and wings (light form). In central Saskatchewan, where both forms occur, the main emergence of dark form adults is earlier in the year than that of light form adults. Comparison of male genitalia of the two forms revealed differences in structure of claspers and aedeagus. In the dark form, claspers lack a prominent ventrocaudal lobe (Fig. 1), and the aedeagus, in caudal aspect, is symmetrical (Figs. 5, 7). In the light form, claspers possess a prominent ventrocaudal lobe (Fig. 3), and the aedeagus is asymmetrical, in caudal aspect (Figs. 6, 8). Differences in form of male genitalia between two forms of putative *O. avara* associated with differences in general body coloration, and timing of adult emergence, suggested to us that we were studying not just variants of a single species, but two distinct species. We then searched for differences in other life stages.

We were able to associate adult females, larvae, and pupae with males of the dark and light forms, respectively, and morphological differences were found which discriminate between them.

We also examined '*O. avara*' specimens loaned to us by Dr. G. B. Wiggins of the Royal Ontario Museum (ROM). These had been collected from 11 North American localities outside Saskatchewan. The dark form was recorded from eight localities, the light form from three; there was no overlap. Adults of dark and light forms from the 11 localities are morphologically consistent with adults of their equivalents from Saskatchewan. Presence of dark and light forms in collections of '*O. avara*' from localities outside of Saskatchewan indicates that these forms are not local variants, restricted to Saskatchewan, but both are widely distributed in North America. This further strengthened our conclusion that the two forms are distinct species.

The type specimens of *O. avara* and *O. disjuncta*

The two species recognized by us could not be named, based on published information. *O. avara* belongs to the *disjuncta* species group of the genus *Oecetis*. The *disjuncta* group contains three species, *O. elatus* Denning and Sykora, *O. avara* (Banks), and *O. disjuncta* (Banks). Taxonomic status of *O. disjuncta* has remained in doubt since Ross (1944) suggested that this form might be conspecific with *O. avara*. Drawings of the male genitalia of *O. avara* (Ross, 1944), and of *O. disjuncta* (Banks, 1920) indicate that males of both species have a prominent ventrocaudal lobe on the clasper, but that the dorsal region of the clasper in *O. disjuncta* is much larger than it is in *O. avara*. Ross (1938), however, stated that the male genitalia of the type specimens of *O. avara* and *O. disjuncta* were very similar, which suggested to us that

Banks' (1920) drawing of the clasper of *O. disjuncta* might be inaccurate.

We examined the genitalia of male type specimens of *O. avara* and *O. disjuncta*, and found that each clasper of the holotype of *O. avara* has a prominent ventrocaudal lobe. The clasper of the lectotype male of *O. disjuncta*, however, lacks a prominent ventrocaudal lobe, although Banks' (1920) drawing of the genitalia of *O. disjuncta* illustrated this lobe. Also, the dorsal portion of the clasper of the type specimen of *O. disjuncta* is not markedly enlarged, although Banks' drawing indicated it to be so. The aedeagus of the *O. avara* holotype is damaged and its structure could not be determined. The aedeagus of the type specimen of *O. disjuncta* is symmetrical, in caudal aspect.

Our study of the genitalia of the two forms revealed that male specimens were most effectively discriminated between by differences in aedeagal structure. Differences in clasper shape were useful for separating most specimens, but not for discriminating between a few specimens which had claspers intermediate in structure. Form of claspers and aedeagus of the *O. disjuncta* lectotype resemble those of males of the dark form. On this basis we concluded that the dark form was conspecific with *O. disjuncta*. Although the aedeagus of the *O. avara* holotype is damaged, and could not be compared to males of the light form, the claspers, with their prominent ventrocaudal lobes, leave no doubt that *O. avara* is conspecific with the light form of our study. We conclude that *O. disjuncta* and *O. avara*, are taxonomically distinct.

DESCRIPTIONS

This section is divided into two parts. In the first, selected morphological features of adults, larvae, and pupae of *O. disjuncta* and *O. avara* are discussed, to facilitate accurate identification of specimens and to provide comparative information about interspecific variation in certain structures. The second part provides detailed descriptions of adults, larvae, and pupae of *O. disjuncta* and *O. avara*.

Descriptions are based on examination of a large number of specimens in our collection taken throughout the province of Saskatchewan, as well as some from the ROM.

Comparison of selected features

Adults. – Although most adults of *O. avara* are yellow, and adults of *O. disjuncta* dark brown, some are intermediate. The tibial spur formula of *O. disjuncta* and *O. avara* is 1,2,2 which distinguishes these two species from the closely related *O. elatus* which, according to Denning and Sykora (1966), has a spur formula of 1,2,3.

The only feature of the male genitalia which is consistently different in the two species is structure of the aedeagus. In caudal aspect, the aedeagus of *O. disjuncta* is symmetrical (Figs. 5, 7), while in *O. avara* it is asymmetrical (Figs. 6, 8). There are no sclerotized areas on the apico-dorsal surface of the aedeagus in *O. disjuncta* (Figs. 5, 7), while in *O. avara* sclerotized areas are present on that region (Figs. 6, 8). Form of the claspers differs in the two species. Most males of *O. disjuncta* lack a prominent ventrocaudal lobe (Fig. 1), while males of *O. avara* have such a lobe (Fig. 3). However, in both species, some males have claspers that are nearly intermediate. Ventral margins of bases of claspers in the normal resting position are more widely separated in *O. avara* (Fig. 13) than they are in *O. disjuncta* (Fig. 12). The median process of tergum X consists of one (Fig. 10) or two (Fig. 9) lobes in *O. disjuncta*. Since both variants are represented in many series of males collected on the same date at the same locality,

and since no other morphological differences were detected between males with one or two lobes, we conclude that these variants are conspecific. In males of *O. avara* examined in this study the median process of tergum X is a single lobe (Fig. 11).

We identified some morphological differences between female genitalia, but it is uncertain if these will distinguish between all specimens. Sternum IX of females of both species has a similar pattern of coloration but, in *O. disjuncta*, the darkened area is much darker (Fig. 14) than in *O. avara* (Fig. 15). Body coloration is varied; possibly specimens will be found in which sternal color is intermediate, although we have not seen such intermediates. The lateral sclerite of segment IX also differs in shape in the two species. In *O. avara* (Fig. 17) the caudal margin of this sclerite is produced as a prominent ventrocaudal lobe, projected beyond the caudal margin of sternum IX in ventral aspect (Fig. 15). In *O. disjuncta* the ventrocaudal lobe of the lateral sclerite of segment IX is slightly developed or absent (Fig. 16) and, in ventral aspect (Fig. 14), this lobe does not project beyond the caudal margin of sternum IX. However, some females of *O. disjuncta* have a prominent ventrocaudal lobe on the lateral sclerite of segment IX. Although some females of *O. avara* and *O. disjuncta* may prove difficult to identify, most specimens can be readily separated using the features discussed above.

Larvae. – Larvae of *O. avara* and *O. disjuncta* are morphologically similar and, currently, only mature larvae of these two species can be assigned to species. The ventral apotome of the head capsule is much narrower, relative to its length, in *O. disjuncta* (Fig. 23) than in *O. avara* (Fig. 24). Difference in shape of the ventral apotome in larvae of these two species is reflected by difference in value of the width/length ratio for the ventral apotome of each species. Values for *O. disjuncta* are 1.7 – 2.8 ($\bar{x} = 2.23$) and for *O. avara* 3.14 – 8.00 ($\bar{x} = 4.48$). Head color differs between most specimens of *O. avara* and *O. disjuncta* but intermediate specimens were observed for both species. The dorsum of the head capsule in most specimens of *O. disjuncta* is brown, marked by darker muscle scars (Figs. 18, 21), while in *O. avara* the head capsule is yellow, with muscle scars not contrasted with the ground color (Figs. 19, 22). In *O. disjuncta* larvae the dorsal setae of the distal articles of the thoracic legs (Figs. 33, 34) tend to be longer relative to the width of the parent article than are the equivalent setae in *O. avara* larvae (Figs. 35, 36).

Pupae. – Pupae of *O. avara* and *O. disjuncta* are morphologically very similar. The only distinguishing feature is relative length of four setae on front of head. In *O. disjuncta* (Fig. 38) the ventral pair of setae are shorter than the dorsal pair. In *O. avara* these four setae are subequal (Fig. 39).

Detailed descriptions

Oecetis disjuncta (Banks)

Oecetina disjuncta Banks, 1920: 351 (Type locality: California, Arroyo Seco Canyon, San Gabriel Mountains).

Adults. – Body and wings brown, legs yellow. Forewing with dark patches on stigma, at base of discoidal and of thyridial cells, on chord, at branching point of Cul, at juncture of anal and cubital veins, and at extremities of veins extended to wing margin. Tibial spur formula 1,2,2. Males 11–12 mm, females 10 – 12 mm in length.

Male abdominal segment IX annular; in lateral aspect (Fig. 1), dorsal half wider than ventral half, numerous setae on lateral surface; sternum, ventrally (Fig. 12), with large membranous area; cercus short, tubular (Fig. 1) or elongate with ventral surface concave. Clasper (Fig. 1), in lateral aspect, with dorsal margin rounded, posterior margin shallowly emarginate, ventrocaudal lobe reduced or absent; few specimens with posterior margin emarginate and ventrocaudal lobe present; ventromesal margins of both claspers, close together (Fig. 12). Segment X with pair of lightly sclerotized, triangular lateral lobes; mesal process of one (Fig. 10) or two (Fig. 9) lobes (in dorsal aspect), apex of lobes entire (Fig. 9) or incised (Fig. 10). Aedeagus, in lateral aspect (Fig. 2), with distal half directed ventrad; in caudal aspect (Figs. 5, 7), symmetrical, posterodorsal surface entirely membranous; internal sclerotized ring symmetrical in caudal aspect (Fig. 7).

Female genitalia with lateral sclerite of segment IX narrow (Fig. 16); ventrocaudal lobe absent or slightly developed, not extended beyond caudal margin of sternum IX (Fig. 14); few specimens with caudal lobe well developed, extended beyond caudal margin of sternum IX. Latter with ventral surface in form of raised, flattened, oval area (Fig. 14); pattern on oval area darker and more distinct than in *O. avara*, oval area bordered by dark area anteriorly and laterally. Cercus, in lateral aspect (Fig. 16), evenly rounded apically, short, not extended beyond segment X. Clasper, in lateral aspect (Fig. 16), rectangular, with ventral and dorsal margins thickened. Segment X mostly membranous; ventrocaudal margin sclerotized, extended beyond rest of segment. Bursa copulatrix as in Figure 14.

Larva. – Head with dorsum dark yellow to brown, marked by darker spots (Figs. 18, 21); anterolateral region brown (Fig. 21), area about eyes white; lateral and posterolateral regions white except scattered brown spots (Fig. 21) and large brown area in middle of gena with few darker spots; venter of head (Fig. 23) light except brown ventral apotome, pair of brown triangular patches posterad of ventral apotome, and dark rim around occipital foramen. Cephalic seta 13 ventrad of midpoint between setae 14 and 15 (Fig. 18); seta 16 directly anterad of seta 17. Frontoclypeal apotome (Fig. 18) darkest laterally; posterior part with two large brown spots, one behind other, subdivided in some specimens; anterior part of frontoclypeal apotome with two pairs of brown spots; linear pale area between each anterolateral corner and rest of apotome (Figs. 18, 20). Each parietal sclerite (Fig. 18) with four brown spots along dorsomesal margin; more brown spots near margin with subocular line. Structure of labrum as in *O. avara*, spines of ventral comb as in Figure 29. Mandibles (Fig. 26) each with single blade, mesal margin basad of subapical teeth of most specimens without serrations. Plate on dorsal surface of submentum V-shaped (Fig. 25), with point of V directed caudad. Ventral apotome (Fig. 23) nearly as wide as long (width/length ratio values range 1.7–2.8; (\bar{x} = 2.23; n = 40); lateral margins of apotome rounded, anterolateral extensions present.

Pronotum (Fig. 32) with light anterior transverse band; middle with light brown transverse band; posterior region light, marked by few brown spots. Each mesonotal sclerite (Fig. 32) brown anteriorly, lighter posteriorly; one seta near anteromesal corner, 16 to 21 setae along anterior and lateral margins, three setae on middle of sclerite. Metanotum (Fig. 32) with sa2 of one to two setae; sa2 of one to three setae. Trochantin of propleuron (Fig. 30) with three to six setae on dorsal surface. Mesopleuron with single seta on each of episternum and epimeron. Metapleuron (Fig. 32) with as many as eight setae on episternum, one seta on epimeron. Foreleg (Fig. 33) without secondary setae on ventral surface of basal part of trochanter; anterior surface of apex of trochanter with two stout, spine-like setae on ventral surface, two

setae near distal oblique margin; setae on dorsal surface of femur longer relative to femur width than in *O. avara*; tibia with single spine-like seta on distal portion of anterior surface; claw as in *O. avara*. Structure of midleg and hindleg (Fig. 34) similar to *O. avara* except setae on dorsal surfaces of femur and tibia of these legs longer relative to width of article than in *O. avara*. Mesosternum without setae. Metasternum with two or three setae (in few individuals).

Abdomen with anterior gills on dorsum of segments II to VII and venter of segments II to VI; pair of pleural gills on segment II; gills absent from lateral lobes of segment I. Segment I with two groups of hooked spines at tip of median dorsal lobe (Fig. 32), each group wider than long. Segment IX with single seta near each lateral margin; posterior margin with six long and four short setae (Fig. 31). Hairs and spines sparse on membranous caudal surface of abdomen. Claw of anal proleg with two dorsal denticles.

Mature larvae 7–8 mm in length.

Pupa. – Labrum (Fig. 40) rounded, triangular; anterior margin extended anterad mesally as short, acute lobe. Mandibles (Fig. 37) with distal quarter of length directed slightly mesad; mesal margin with teeth in region of bend, fine serrations basad and distad of teeth; two lateral setae about equal in length, in line along lateral margin of mandible. Frons with two pairs of setae; ventral pair much shorter than dorsal pair (Fig. 38).

Abdomen with anterior tergal plates on segments III to VII dark brown (Fig. 41), each with three to five teeth; posterior part of each plate directly posterad of midline of anterior part of plate in most specimens; anterior part of each plate oval, with anterior margin rounded, anterior part rounded-triangular in few specimens; posterior tergal plate of segment V oval, teeth inserted anterad of thin lighter area near posterior margin of plate. Lateral sclerotized bars on each side of terga II to VIII T-shaped (Fig. 43), bars of most specimens thicker than in *O. avara*. Anal rod as in Figure 45.

Pupae of both sexes 8 mm in length.

Larval and pupal cases. – Larval cases of *O. disjuncta* are tubular, curved slightly posteriorly, and composed of sand grains (Figs. 46, 47). Cases of younger larvae (Fig. 46) are more markedly tapered and curved than those of mature larvae (Fig. 47). The pupal case (Fig. 48) is similar to that constructed by mature larvae except that anterior end of pupal case has a prominent flange. Pupal cases of *O. avara* do not have this prominent flange at the anterior end.

Bionomics. – Larvae of *O. disjuncta* occur primarily in fast flowing boreal streams. Adults were collected in Saskatchewan from June 16 to June 21, and pupae from May 23 to July 17. There is a single generation per year, the larvae overwintering. Adult emergence periods of *O. avara* and *O. disjuncta* overlap but the peak emergence for *O. disjuncta* occurs earlier than for *O. avara*.

Distribution. – *O. disjuncta* is recorded from Saskatchewan in Canada, and from Michigan, South Dakota, Utah, Oregon and California in the United States. In Saskatchewan, *O. disjuncta* is restricted to rivers in the central and northern regions of the province (Fig. 50).

Material examined. – SASKATCHEWAN Cold R. at Cold L., 10.VII.1975, 1 larva–30.VIII.1976, 2 larvae; Mistohay Cr. at Hwy. 224, 12.VIII.1975, 3 larva–23.V.1975, 1 larvae, 2 ♂ pupae; Arsenault R. at Hwy. 104, 23.V.1975, 4 pupae, 6 larvae; Englishman R. at Hwy. 26, 2.V.1977, 4 larvae–22.V.1975, 3 ♀ pupae–12.VIII.1975, 8 larvae–21.VIII.1977, 2 larvae–29.VIII.1976, 14 larvae; Waterhen R. at Hwy. 26, 4.V.1977, 9 larvae–23.V.1975, 2 larvae–25.VII.1976, 29 larvae; Waskesiu L., 4.VII.1940, 1 ♀; Weyakwin R. at Hwy. 2, 29.VII.1976, 5 larvae; Montreal R., 8.V.1960, 10 larvae–7.VI.1960, 1 larva–22.VIII.1960, 3 larvae; Caribou Cr. at Hwy. 120, 6.VIII.1976, 5 larvae–29.V.1977, 3 ♀ pupae–12.IV.1977, 1 larva–17.VI.1976, 4 ♂ –11.VIII.1977, 1 larva–15.VII.1976, 3 larvae; McDougal Cr. at Hwy. 120, 31.V.1977, 3 larvae, 5 pupae–5.V.1977, 6 larvae–17.VI.1977, 2 ♂ –22.VI.1977, 2 larvae, 2 ♀ pupae, 1 ♂ pupa–7.VIII.1976, 9 larvae–16.VI.1976, 15 ♂ –18.VI.1976, 1 ♀, 15 ♂ –7.VII.1977, 1 ♂ –21.IX.1976, 13 larvae; Puskwakau R. at Hwy. 106, 10.VI.1975, 1 larva–17.VII.1975, 1 ♂ pupa–6.VIII.1976, 6 larvae; Cub Cr. at Hwy. 106, 29.V.1975, 1 larva; Torch R. at Hwy. 106, 21.IX.1976, 3 larvae; MacKay Cr. at Hwy. 2, 5.VI.1974, 3 larvae–7.VI.1977, 1 ♀ pupa–8.VI.1977, 1 ♂ pupa, 1 ♀

pupa—21.VI.1976, 1 ♀—30.VII.1976, 9 larvae—18.VIII.1976, 11 larvae; Waddy R. at Hwy. 102, 3.VII.1975, 2 ♀; Creek at mi. 37 of Hwy. 105, 17.VIII.1976, 8 larvae; River at mi. 85 of Hwy. 102, 7.VIII. 1972, 2 larvae; CALIFORNIA—stream near Oregon City, Butte Co., 1.VI.1961, 1 ♂(ROM); OREGON—South Umpqua R. at mouth of Coffee Cr., Rt. 138, s. Kellogg, Douglas Co. 7.VI.1968, 2 ♂ (ROM); Lake Co., Deep Creek 56, 13.VI.1978, 2 ♂ (ROM); Lake Co. Twenty-mile Cr., Site 6+7, 6.VI.1978, 14 ♂(ROM); SOUTH DAKOTA—stream in Spring Cr. Campground, Black Hills near Rapid City, 17.VI.1969, 2 ♂ (ROM); Horse Cr. at Sheridan L., Pennington Co., 8.VI.1961, 5 ♂ (ROM); MICHIGAN—Pellston, Emmet Co., west branch Maple R. at Rt. 31, 13.VI. 1972, 2 larvae, 1 pupa (ROM); UTAH—Bear R., East Fork For. Campground, Summit Co., 12.VI.1961, 6 , 2 (ROM).

Oecetis avara (Banks)

Setodes avara Banks, 1895: 316. (Type locality: Sherbrooke, Canada). *Oecetina avara* Banks, 1899: 214.

Adults. — Body and wings yellow to light brown, legs yellow. Forewing with spots as in *O. disjuncta*, spots sometimes absent in females. Tibial spur formula 1,2,2. Males 9.5–11 mm, females 7–10 mm in length.

Male genitalia with segment IX annular; in lateral aspect (Fig. 3), dorsal half wider than ventral half, setae on lateral surface not as numerous as in *O. disjuncta*; sternum, in ventral aspect (Fig. 13), with large membranous area; cercus (Fig. 3) with dorsal surface convex, ventral surface concave. Clasper (Fig. 3) with dorsal margin rounded, posterior margin deeply incised, shallowly incised in few specimens; ventrocaudal lobe prominent, not as prominent in few specimens; ventromesal margins of both claspers widely separated at base (Fig. 13). Segment X (Fig. 11) with pair of lightly sclerotized triangular lateral lobes; mesal process composed of single elongated, sclerotized lobe, apex of lobe entire (Fig. 11) or shallowly incised (Fig. 10). Aedeagus, in lateral aspect (Fig. 4), curved posteroventrad; in caudal aspect (Figs. 6, 8) aedeagus asymmetrical, apicodorsal surface with distinct sclerotized areas; inner sclerotized ring asymmetrical (Fig. 8).

Female genitalia with lateral sclerite of segment IX, in lateral aspect (Fig. 17), narrow, with prominent ventrocaudal lobe; lobe extended beyond caudal margin of sternum IX (Fig. 15); latter with ventral surface in form of raised, flattened oval area (Fig. 15); pattern on oval area much lighter and less distinct than in *O. disjuncta*; oval area bordered by dark area laterally and anteriorly. Cercus, in lateral aspect (Fig. 17), rounded, triangular, not extended beyond segment X. Claspers and segment X (Fig. 17) as in *O. disjuncta*. Bursa copulatrix as in Figure 15.

Larva. — Dorsum of head yellow (Fig. 19); muscle scars indistinct; darker in color and contrasted with ground color of head in few specimens. Posterolateral and posterodorsal areas of head white (Fig. 22). Cephalic seta 13 (Fig. 19) directly below midpoint between seta 14 and 15; seta 17 directly posterad of seta 16. Frontoclypeal apotome with linear pale area between each anterolateral corner and rest of sclerite (Figs. 19, 20). Labrum (Fig. 28) with convex lobe on either side of mesal indentation; margin of lobe entire; numerous secondary setae on anterior portion of dorsum; venter with pair of setae near lateral margin and single seta near anterior margin on each side, some small spine-like hairs near anterior seta on left side, prominent comb of spines near posterior margin, spines as in Figure 29. Mandibles (Fig. 27) single bladed, prominent serrations on mesal surface basad of subapical teeth. Sclerite on dorsal surface of submentum V-shaped or U-shaped, point of V or U directed posterad. Ventral apotome (Fig. 24) yellow, rectangular, much wider than long (width/length ratio values 3.14 – 8; \bar{x} = 4.48; n = 37); lateral margins rounded, anterolateral extensions present. Pair of triangular sclerites posterad of caudal margin of ventral apotome.

Thorax similar to *O. disjuncta* (Fig. 32). Pronotum with light yellow transverse band anteriorly, darker transverse band in middle, posterior portion white, marked by few light brown spots. Each mesontal sclerite dark yellow anteriorly, white posteriorly, single seta near anteromesal corner, as many as 19 setae on anterior and lateral portions of sclerite, three setae on middle of sclerite. Metanotum with sa2 and sa3 each of single seta. Structure of trochantin of propleuron as in *O. disjuncta*, as many as seven setae on dorsal surface. One to three setae on mesoepisternum; one seta on mesoepimeron. As many as seven setae on metaepisternum; one seta on metaepimeron. Foreleg (Fig. 35) without secondary setae on ventral surface of basal part of trochanter; anterior surface of apical part of trochanter with two stout spine-like setae on ventral surface, two setae near distal oblique margin of trochanter; setae on dorsal surface of femur shorter relative to femur width than in *O. disjuncta*; tibia with single spine-like seta on distal portion of anterior surface; claw about as long as tarsus. Midleg with few spine-like setae and finer setae on ventral surface of femur; most setae on dorsal surfaces of femur and tibia shorter than in *O. disjuncta*; claw shorter than tarsus, basal seta well developed. Hindleg (Fig. 36) with most setae on dorsal surfaces of femur and tibia shorter than in *O. disjuncta*; tibia and tarsus each with spine-like setae on ventral surface; claw shorter than tarsus, basal seta well developed. Mesosternum without setae, metasternum with pair of setae.

Abdomen with anterior gills on segments II to VI or VII dorsally and ventrally; one pair of pleural gills on segment II; in few specimens, gill on dorsal surface of lateral lobe of segment I. Two groups of hooked spines at tip of median dorsal lobe of segment I as in *O. disjuncta*. Segment IX with seta on each side of tergum near lateral margin, posterior margin of tergum with six large and four small setae. Hairs and spines sparse on surface of caudal end of abdomen. Claw of anal proleg with two dorsal denticles.

Mature larvae 6.5 – 9 mm in length.

Pupa. – Anterior surface of head with two pairs of setae subequal (Fig. 39). Abdomen with anterior hook-bearing plates on terga of segments III to VII (Fig. 42) yellow to light brown; anterior portion of each plate triangular, anterior end of triangle in most specimens directed laterad of midline of posterior portion of plate. Lateral bars on terga of segments II to VIII (Fig. 44) in most specimens not as wide as in *O. disjuncta*. Other features of *O. avara* pupa similar to those already described for pupa of *O. disjuncta*.

Male pupae 6 – 9 mm in length, female pupae 6 – 7 mm.

Larval and pupal cases. – The larval case of *O. avara* is similar to that of *O. disjuncta*. Some pupal cases of *O. avara* (Fig. 49) have some sand grains attached around the rim of the anterior end of the case but the case lacks the prominent flange at the anterior end characteristic of those of *O. disjuncta*.

Bionomics. – Larvae of *O. avara* inhabit turbid waters of the Saskatchewan River system as well as clear, fast-flowing streams in the boreal forest region of Saskatchewan. In Saskatchewan, adults of *O. avara* were collected from June 16 to August 12. In cooler boreal streams, pupae of *O. avara* were collected from May 29 to July 15. This species is univoltine in these streams. In the warmer waters of the Saskatchewan River system *O. avara* pupae were collected in mid-summer and in fall, which suggests that this species is bivoltine in these warmer waters. The larva is the overwintering stage in this species.

Distribution. – *O. avara* is recorded throughout North America, from southern Canada to Mexico (Ross, 1944). However, all previously published records are suspect since specimens of *O. disjuncta* may have been incorrectly identified as *O. avara* in previous publications. In this study we examined specimens of *O. avara* from Saskatchewan and Ontario in Canada, and

from Idaho and Montana in the United States.

In Saskatchewan *O. avara* larvae live in the main branches of the Saskatchewan River system and are also common in streams in the boreal forests of the central region of the province (Fig. 50) but they are absent from northern Saskatchewan.

Material examined. – *SASKATCHEWAN* South Saskatchewan R., 1/4 mi. upstream from the Queen Elizabeth Power Station, 11.VI.1972, 1 ♀ pupa–10.VII.1972, 8 ♂–12.VII.1971, 1 ♂–13.VII.1971, 1 ♂, 2 ♀ –15.VII.1972 4 ♂, 1 ♀ –19.VII.1971, 2 ♂ –23.VII.1972, 1 ♂ –15.VII.1971 1 ♂ ;South Saskatchewan R., ferry e. of Hague, 21.VI.1972, 1 ♂ –4.VII.1972, 4 ♂ ; South Saskatchewan R., ferry no. of Birch Hills, 26.V.1972, 7 larvae–25.V.1973, 10 larvae–7.VI.1972, 2 ♂ pupae, 2 ♀ pupae, 2 larvae–12.VI.1972, 1 ♀ pupa, 13 ♂ –24.IV.1973, 4 larvae–6.VII.1972, 2 ♂, 1 ♀ –21.IX.1972, 1 larva–20.VI.1973, 12 larvae–18.VII.1972, 1 ♀ –17.VIII.1971, 6 larvae–8.V.1973 1 larva; South Saskatchewan R., ferry n. of Lemsford, 14.VII.1971, 3 ♂ pupae, 2 ♀ pupae–12.VII.1972, 2 ♀, 2 ♂, 3 ♂ pupae, 3 ♀ pupae–24.VII. 1972, 2 ♂ pupae, 3 ♀ pupae, 1 larva–6.IX.1972, 1 ♀ pupa–27.IX.1972, 1 larva–25.VI.1972, 1 larva; North Saskatchewan R., ferry 10 mi. e. of Prince Albert, 14.IX.1972, 2 larvae–17.V.1972, 1 larva–15.VI.1972, 13 ♂, 5 ♀ –21.IX.1972, 1 larva–15.VI. 1972, 1 ♀ ; North Saskatchewan R. at Hwy. 3, 23.VI.1972, 9 ♂, 7 ♀ ; North Saskatchewan R. at Hwy. 5, 23.VIII.1972, 10 larvae; North Saskatchewan R., Prince Albert, 20.VI.1973, 1 ♂ pupa; Montreal R. at Hwy. 2, s. of La Ronge, 27.VI.1972, 7 ♂, 3 ♀, 1 larva–11.VI.1976, 6 ♂, 5 ♀ –16.VI.1971, 6 ♂ –19.VI.1976, 1 ♂ ; Montreal R., 28.V.1969, 1 larva–20.VII.1960, 1 ♂ –15.VII.1960, 1 larva–28.VII.1960, 5 larvae–22.VI.1960, 5 larvae–11.VIII.1960, 16 larvae; Montreal R. at outflow of Bigstone Lake, 4.V.1977, 2 larvae–10.VI.1976, 3 larvae–6.VII. 1977, 1 larva, 4 pupae; Nipekamew R. at Hwy. 165, 16.VII.1975, 1 ♂, 1 ♀ –13.VII.1976, 2 ♂, 3 ♂ pupae, 1 ♀ pupa, 5 larvae; Weyakwin R. at Hwy. 2, 28.VI.1976, 11 ♂ –11.VI.1976, 2 larvae, 4 pupae–16.VI.1976, 1 ♂ –4.VII.1975, 1 larva–11.VII.1976, 1 ♂ pupa, 1 ♀ pupa–14.VII.1974, 1 ♀, 1 ♂ –16.VII.1975, 3 ♂, 2 ♀ ; Caribou Cr. at Hwy. 120, 29.V.1977, 3 ♂ pupae, 17 larvae–17.VI.1977, 1 ♀ pupa, 2 larvae–12.IV.1976, 3 larvae–16.VII.1977, 1 ♂, 1 ♀ –23.VI.1977, 9 ♂, 12 ♀, 3 larvae–17.VI.1976, 3 ♂, 2 ♀, 5 larvae–27.VI.1977, 1 ♂ pupa–13.VII.1977, 28 ♂, 16 ♀, 1 ♂ pupa–15.VII.1976, 1 ♂ pupa, 1 ♀ pupa, 35 ♂, 28 ♀, 5 larvae–7.VII.1977, 1 larva, 2 ♂ pupae, 1 ♀ pupa–23.VI.1977, 1 ♂ pupa, 1 ♂, 2 ♀ –6.VIII.1976, 4 ♂, 9 larvae–27.VI.1977, 1 prepupa–15.VII.1976, 3 prepupae–17.VII.1976, 1 larva; Crean R. at Hwy. 2, 9.VI.1976, 1 ♂ pupa; Torch R. at Hwy. 106, 26.IV.1977, 1 larva–16.VI.1976, 2 ♂ –2.VII.1975, 1 ♂ –15.VII.1976, 1 ♂, 2 ♀ –5.VIII.1976, 4 ♂, 2 larvae–21.IX.1976, 8 larvae; Mistohay Cr. at Hwy. 224, 10.VII.1976, 38 ♂, 15 ♀, 1 larva–11.VIII.1976, 1 ♂ pupa–12.VIII.1975, 1 ♂ ; Broad Cr. at Hwy. 104 2.VII.1975, 1 ♂, 1 ♀ ; Overflow R. at Hwy. 109, 11.VI.1975, 2 larvae Overflow R., 1958, 1 larva; Taggart Cr. at road to Dore L., 26.VI.1976, 1 ♀ pupa; ONTARIO–Streetsville, Credit River, Peel Co., 23.VII.1952, 4 ♂, 34 ♀ (ROM); MONTANA– Yellow Bay, Flathead L., 26.VII.1965, 1 ♂ ; Missoula Co., Owl Cr., Stn. #4, between Placid L. and Clearwater R., 9.VIII.1973, 13 ♂, 41 ♀ (ROM); IDAHO– 20 mi. s. of Mack's Inn, Fremont Co., 10.VII.1969, 37 ♂, 3 ♀ (ROM).

DISCUSSION

The taxonomic status of *O. disjuncta* has been misunderstood for more than 30 years, for several reasons. First, the description and drawing of the male genitalia of *O. disjuncta* provided by Banks (1920) were inadequate to permit specimens of *O. disjuncta* to be distinguished from specimens of *O. avara*. Second, specimens of the two species are extremely similar morphologically and, even if one can compare type specimens, without a large collection of males of both species to compare with the types it would be difficult to determine the proper taxonomic status of *O. disjuncta*. Third, since Ross (1944) and Denning (1956) suggested that *O. disjuncta* was likely conspecific with *O. avara*, taxonomists have not concerned themselves with clarifying this problem. Specimens of *O. disjuncta* were probably regarded as variants of *O. avara*.

Preliminary evidence suggests that specimens of *O. disjuncta* have previously been identified as *O. avara*. As indicated here, both species are widely distributed in North America, and it seems likely that they are abundant not only in Saskatchewan but, also in many other regions of North America. However, while published records for *O. avara* are numerous, none exist for *O. disjuncta*, except for the type localities. Specimens of *O. disjuncta* have probably been collected but, since they are not published under this or any other name, these specimens must have been identified as *O. avara*. Our study of specimens of *O. avara* from the ROM support this

conclusion. Of 11 vials labelled *O. avara*, lent by the ROM, eight contained specimens of *O. disjuncta*. If misidentifications of specimens of *O. disjuncta* have, indeed, occurred, then some of the published records for *O. avara* are probably incorrect.

Among specimens of the *O. avara* complex which we studied, two species are recognizable: *O. avara* and *O. disjuncta*. However, study of the *O. avara* complex is not complete because we examined specimens from only a limited number of North American localities. Taxonomists should continue careful study of specimens collected at other localities, to determine if additional species are attributable to this complex, or if the morphological differences between *O. avara* and *O. disjuncta* are as clear at these localities as is reported in our study.

DISPOSITION OF MATERIAL

Some adult, larval and pupal specimens of the two *Oecetis* species examined in this study will be deposited in the Royal Ontario Museum, Toronto, and in the Canadian National Collection, Ottawa. The remainder are in the authors' collections, or in the collection of the Entomology Museum, Biology Department, University of Saskatchewan, Saskatoon, Saskatchewan.

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Thanks go also to Dr. Alfred Newton of the Museum of Comparative Zoology for loan of type specimens of *O. avara* and *O. disjuncta*.

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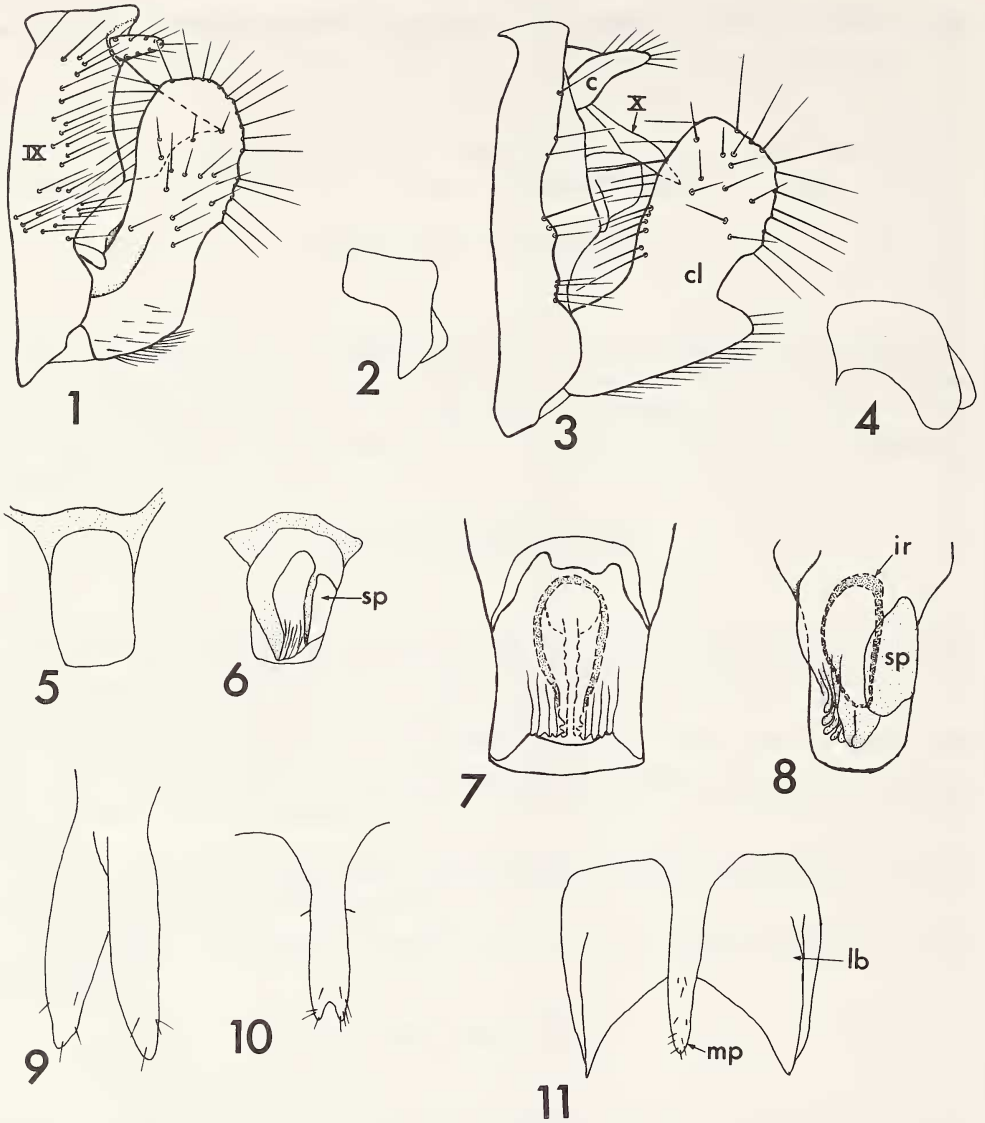


Fig. 1. *O. disjuncta* male genitalia, lateral aspect; Fig. 2. *O. disjuncta* aedeagus, lateral aspect; Fig. 3. *O. avara* male genitalia, lateral aspect, showing cercus (c), and clasper (cl); Fig. 4. *O. avara* aedeagus, lateral aspect; Fig. 5. *O. disjuncta* aedeagus, caudal aspect; Fig. 6. *O. avara* aedeagus, caudal aspect; Fig. 7. *O. disjuncta* enlarged view of aedeagus, caudal (dorsal) aspect, showing internal structure; Fig. 8. *O. avara* enlarged view of aedeagus, caudal aspect, showing sclerotized plate (sp) and internal sclerotized ring (ir); Fig. 9. *O. disjuncta* mesal process of segment X, dorsal aspect; Fig. 10. *O. disjuncta* mesal process of segment X, dorsal aspect; Fig. 11. *O. avara* segment X, dorsal aspect, showing lateral lobe (lb) and mesal process (mp).

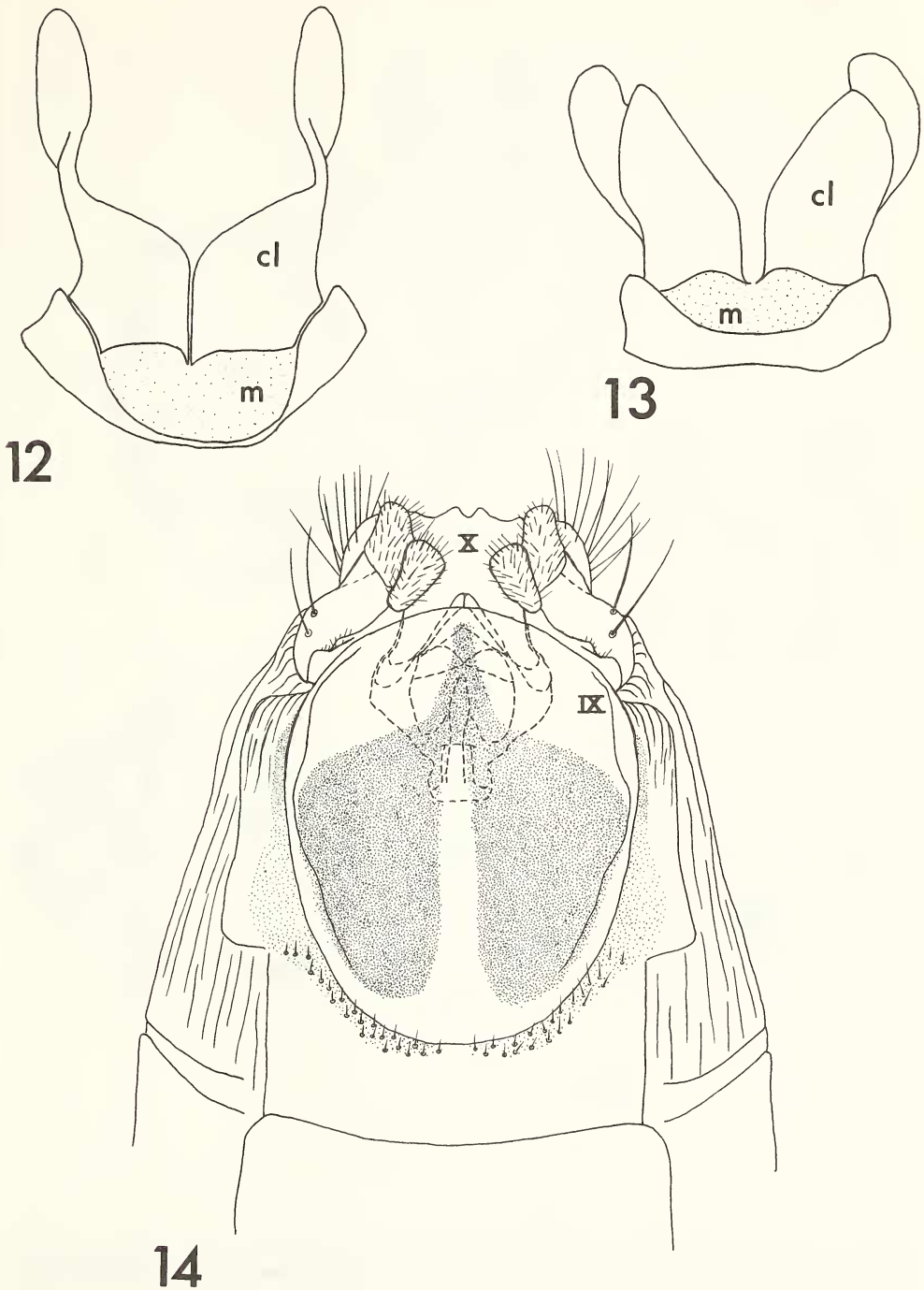
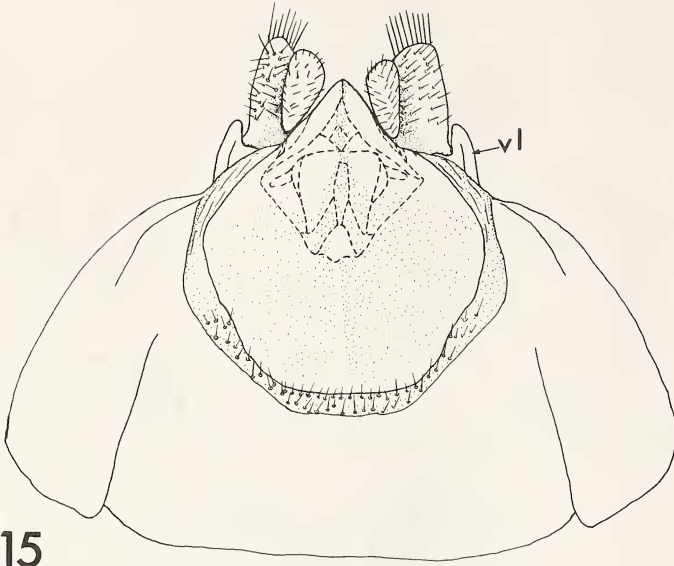
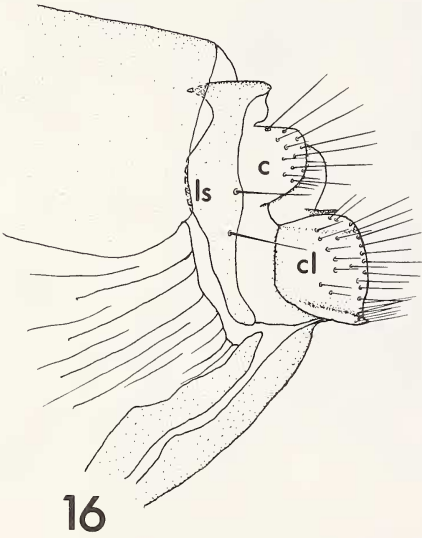


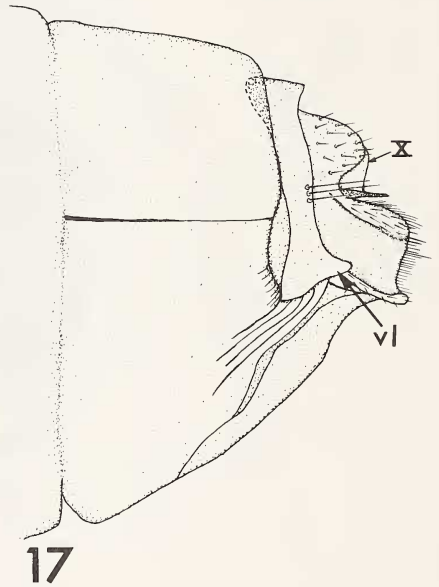
Fig. 12. *O. disjuncta* male genitalia, ventral aspect, showing membranous region (m) of sternum IX, and clasper (cl);
 Fig. 13. *O. avara* male genitalia, ventral aspect, showing membranous region (m) of sternum IX, and clasper (cl); Fig.
 14. *O. disjuncta* female genitalia, ventral aspect.



15



16



17

Fig. 15. *O. avara*, female genitalia, ventral aspect, showing ventrocaudal lobe (vl) of lateral sclerite of segment IX; Fig. 16. *O. disjuncta* female genitalia, lateral aspect, showing lateral sclerite (ls), cercus (c), and clasper (cl); Fig. 17. *O. avara* female genitalia, lateral aspect, showing ventrocaudal lobe (vl) of lateral sclerite of segment IX.

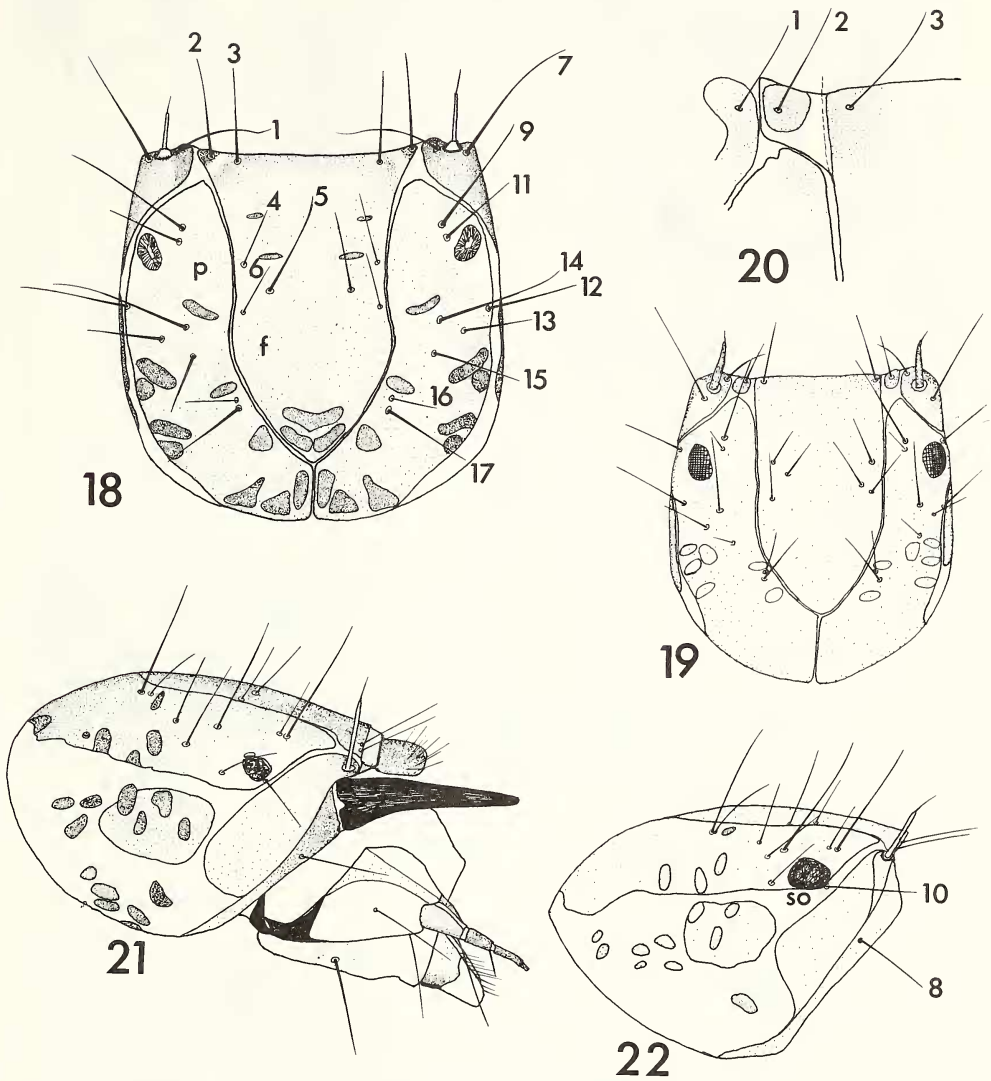


Fig. 18. *O. disjuncta* larval head, dorsal aspect, showing frontoclypeal apotome (f), and parietal sclerite (p); Fig. 19. *O. avara* larval head, dorsal aspect; Fig. 20. *O. avara* view of region in vicinity of anterolateral corner of frontoclypeal apotome; Fig. 21. *O. disjuncta* larval head, lateral aspect; Fig. 22. *O. avara* larval head, lateral aspect, showing subocular line (so).

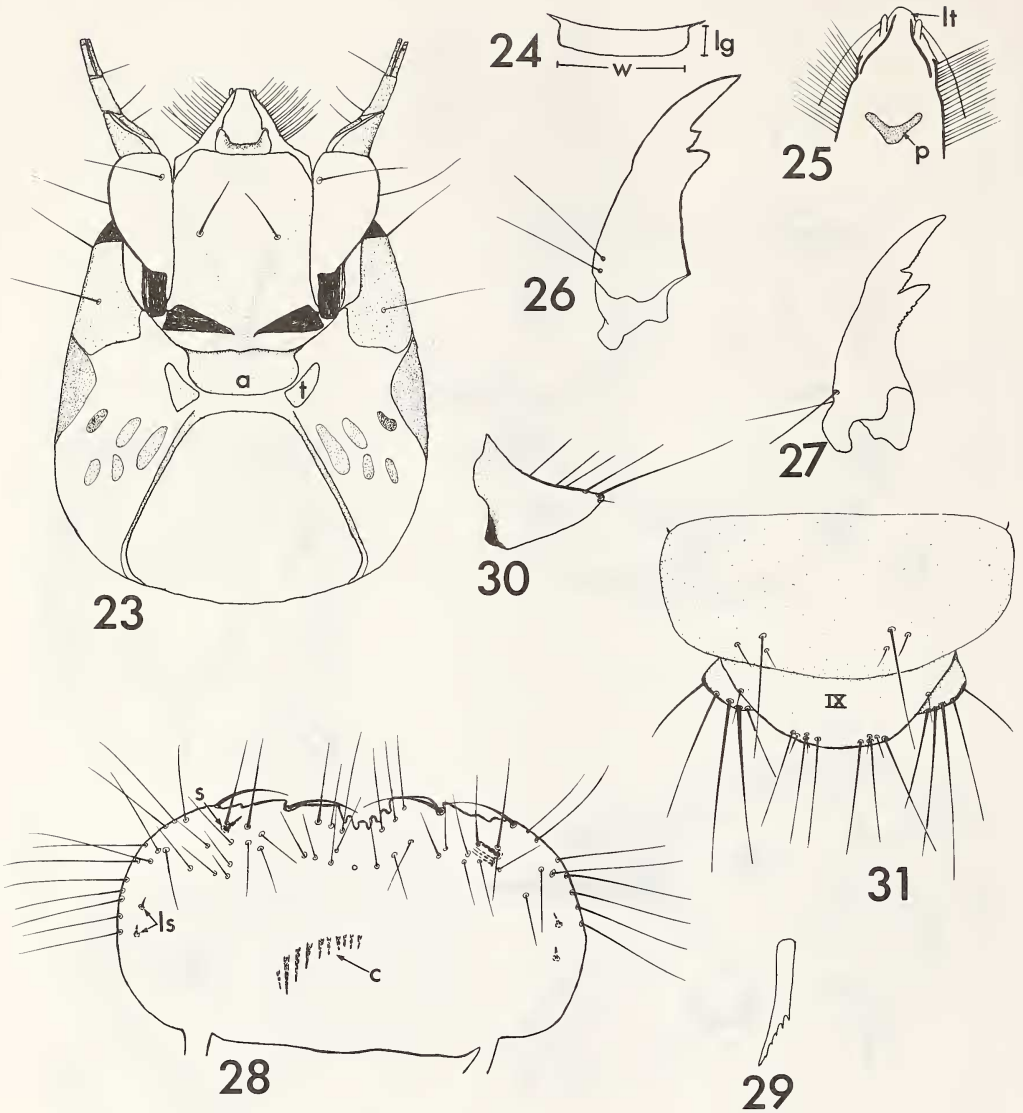


Fig. 23. *O. disjuncta* larval head, ventral aspect, showing ventral apotome (a), and triangular sclerite (t); Fig. 24. *O. avara* ventral apotome, showing width (w), and length (lg) of apotome; Fig. 25. *O. disjuncta* ventral surface of preoral cavity, showing plate (p) on dorsal surface of submentum, and tip of labrum (lt); Fig. 26. *O. disjuncta* larval mandible, dorsal aspect; Fig. 27. *O. avara* larval mandible, dorsal aspect; Fig. 28. *O. avara* labrum, dorsal aspect, showing lateral setae (ls), anterior seta (s), and comb of spines (c), all on ventral surface of labrum; Fig. 29. *O. disjuncta*, one spine from comb of spines on ventral surface of labrum; Fig. 30. *O. disjuncta* trochantin, lateral aspect; Fig. 31. *O. disjuncta* caudal end of abdomen, dorsal aspect.

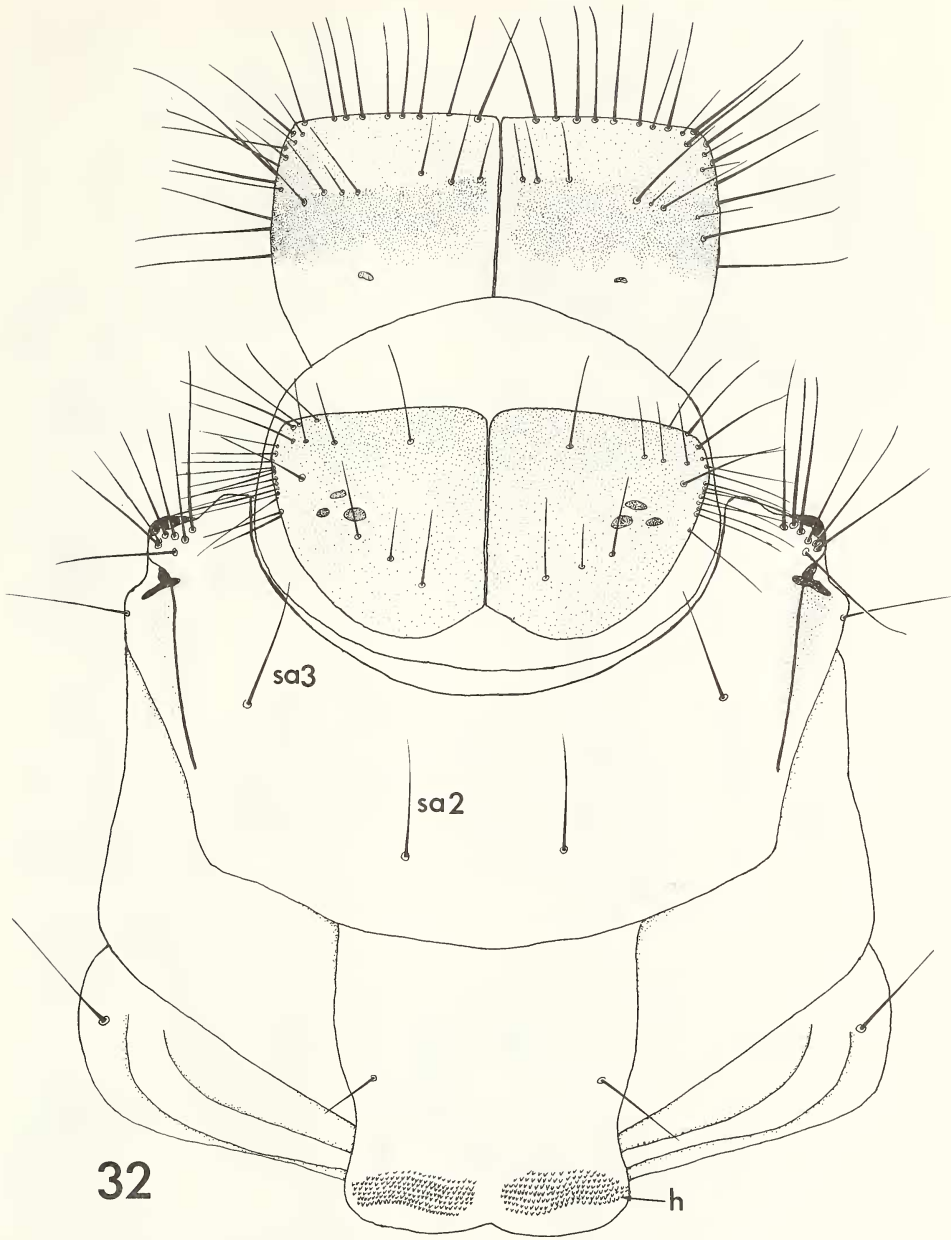


Figure 32. *Oecetis disjuncta* (Banks) thorax and first abdominal segment, dorsal aspect, showing group of hooked spines (h).

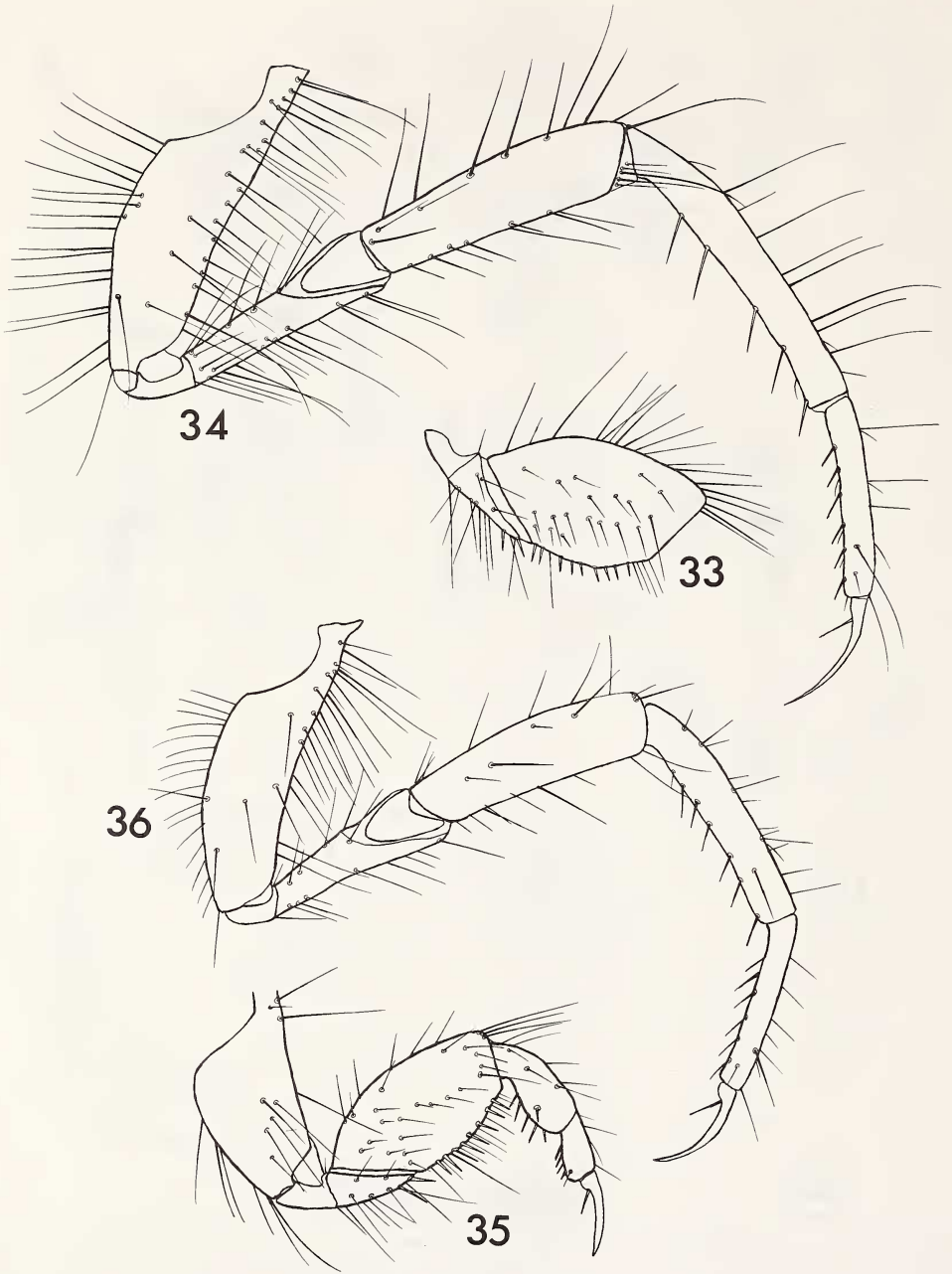


Fig. 33. *O. disjuncta* trochanter and femur of foreleg, anterior aspect; Fig. 34. *O. disjuncta* hindleg, anterior aspect; Fig. 35. *O. avara* foreleg, anterior aspect; Fig. 36. *O. qvara* hindleg, anterior aspect.

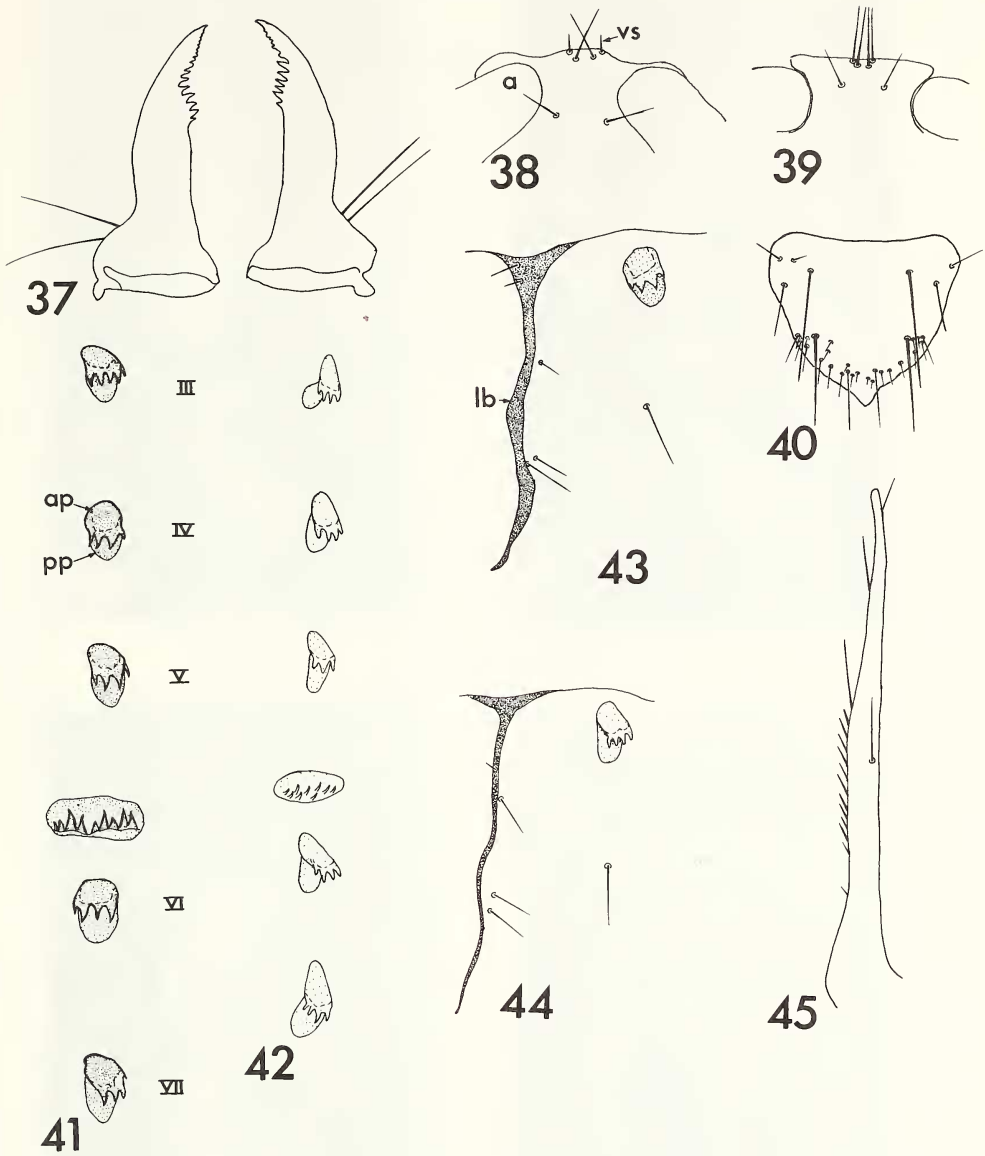


Fig. 37. *O. disjuncta* mandibles, dorsal aspect; Fig. 38. *O. disjuncta* head, anterodorsal aspect, showing antenna (a), and ventral pair of setae (vs); Fig. 39. *O. avara* head, anterodorsal aspect; Fig. 40. *O. disjuncta* labrum, dorsal aspect; Fig. 41. *O. disjuncta* hook-bearing plates on abdominal terga, showing anterior (ap), and posterior parts (pp) of plate; Fig. 42. *O. avara* hook-bearing plates on abdominal terga; Fig. 43. *O. disjuncta* abdominal tergum, showing lateral tergal bar (lb); Fig. 44. *O. avara* abdominal tergum; Fig. 45. *O. disjuncta* anal rod.



Fig. 46. *O. disjuncta* immature larval case, ventral aspect; Fig. 47. *O. disjuncta* mature larval case, ventral aspect; Fig. 48. *O. disjuncta* pupal case, showing flange (f); Fig. 49. *O. avara* pupal case.

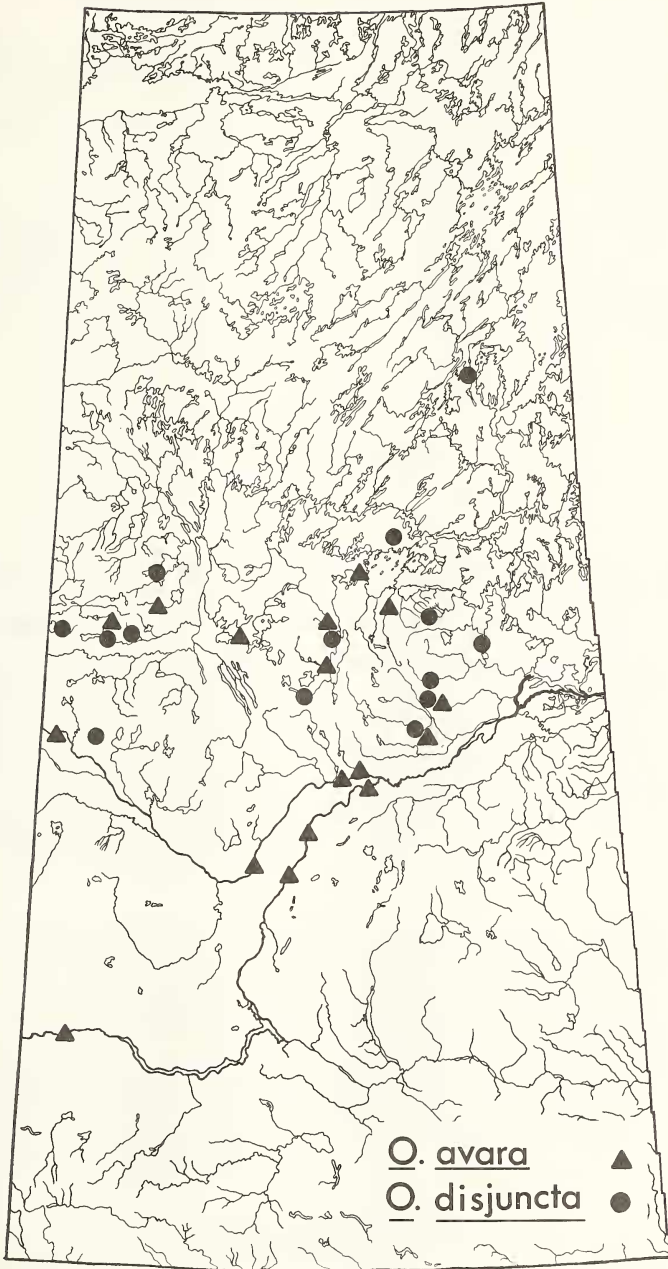


Fig. 50. Distribution of *Oecetis disjuncta* (Banks) and *Oecetis avara* (Banks) in Saskatchewan.

